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On the taxonomy and systematics of the recently described *Lycodon deccanensis* Ganesh, Deuti, Punith, Achyuthan, Mallik, Adhikari, Vogel, 2020 (Serpentes, Colubridae) from India

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Abstract

Lycodon deccanensis Ganesh, Deuti, Punith, Achyuthan, Mallik, Adhikari, Vogel, 2020 was recently described from the Mysore plateau of Karnataka based solely on morphology but lacking in-depth descriptions and comparisons. A scrutiny of the description reveals that the type series, of two specimens, comprise specimens of two different species along with discrepancies throughout the paper. Surveys conducted near the type locality of the species led to the discovery of additional specimens, which allow us to provide an elaborate description of the species and present data on its phylogenetic relationship with members of the genus and comments on the systematics of *Lycodon* of India. Results from molecular phylogenetics suggest that *Lycodon deccanensis* is a member of the *L. aulicus* clade based on molecular data for mitochondrial cytochrome b gene and shows an un-corrected p-distance (sequence divergence) of 14–17% from other members of the *Lycodon aulicus* clade.

Key Words

Cytochrome b, molecular phylogeny, taxonomy, wolf snakes, snake systematics

Introduction

Snakes of the genus *Lycodon* Boie, 1826 commonly called 'wolf snakes', are small to medium-sized colubrids that are generally nocturnal in nature (Whitaker and Captain 2004). They comprise 66 currently recognized species (Wallach et al. 2014, Uetz and Hošek 2020) which are distributed from central Asia and eastern Iran to southern and eastern China and Japan, southwards, across the entire Indo-Chinese Peninsula, and into the Indo-Australian Archipelago and the Philippines (Lanza 1999). The genus has been shown to be paraphyletic and due to the lack of complete sampling in terms of species as well as number of molecular markers, phylogenetic relationships with regard to related genera, especially *Dryocalamus* and *Dinodon* remain unclear (Figueroa et al. 2016, Zaher et al. 2019). In the last five years, eight new species of *Lycodon* + *Dryocalamus* have been described from the countries of Indonesia (Wostl et al. 2017), Laos (Luu et al. 2020), Vietnam (Janssen et al. 2019, Luu et al. 2019), Thailand (Vogel and David 2019), Sri Lanka (Wickramasinghe et al. 2020) and India (Ganesh et al. 2020a). Peninsular India currently has nine recognized *Lycodon* species: *L. aulicus* (Linnaeus, 1758), *L. striatus* (Shaw, 1802), *L. nympha* (Daudin, 1803), *L. gracilis* (Gunther, 1864), *L. anamallensis* Gunther, 1864, *L. travancoricus* (Beddome, 1870), *L. flavomaculatus* Wall, 1907, *L. flavicollis* Mukherjee & Bhupathy, 2007 and the recently described

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Lycodon deccanensis Ganesh, Deuti, Punith, Achyuthan, Mallik, Adhikari, Vogel, 2020. Of these species, *L. aulicus*, *L. anamallensis*, *L. flavicollis*, *L. gracilis*, and *L. striatus* have been recorded from the dry forests of southeastern Karnataka (pers. obs.). Ganesh et al. (2020a) described *Lycodon deccanensis* based on two unsexed specimens BNHS 3596 from Devarayanadurga, Karnataka and ZSI 13271 from South Arcot district, Tamil Nadu. The new species was diagnosed in being distinct from all Indian *Lycodon* in bearing an undivided anal shield and loreal in contact with the internasal. However, a close scrutiny of the description revealed that the paratype ZSI 13271 depicted in fig. 2b of Ganesh et al. (2020a) had loreal shield was not in contact with the internasal and the preocular separated the supraocular and prefrontals a set of character states seen in *L. travancoricus* (Ganesh et al. 2020b, Smith 1943). The description was rather brief, the holotype was not depicted in the publication neither in preserved state nor in life and the sex of the type specimens were not specified. Ganesh et al. (2020a) aimed to resolve the confusion within the Indian *Lycodon*, however, ironically, added more complexity by designating a specimen of *L. travancoricus* (ZSI 13271) as a paratype of the new species. Furthermore, the specimen numbers in the text and figure captions did not match the numbers depicted on the museum tags within the figures (see fig. 4 of Ganesh et al. 2020a) and multiple spellings of *L. travancoricus* were used.

Recent fieldwork conducted near the type locality, yielded additional specimens of *Lycodon deccanensis* that permit us to report additional details of the species and assess its phylogenetic relationships as per current standards in systematics.

Material and methods

Morphology

Two specimens were captured by hand and euthanized with Halothane as per the directive outlined by standard euthanasia protocols (Leary et al. 2013). The specimens were fixed in 4% formalin and later stored in 70% ethanol and deposited in the collection of the National Centre for Biological Sciences (NCBS), Bangalore and the Bombay Natural History Society (BNHS), Mumbai. Measurements were taken with digital calipers to the nearest 0.1 mm and total length was measured using a non-elastic thread with an error of 5 mm.

Morphological data for related species were compared with Smith (1943) and Ganesh and Vogel (2018) and material examined from natural history museums listed below. Ventral scales were counted following Dowling (1951b). The number of dorsal scale rows was counted at approximately one head length behind the head (at 10th ventral), at midbody, and at about one head length before the vent (10th ventral before the cloacal plate), respectively. The dorsal scale reduction formula follows Dowling (1951a) with modifications as proposed by Das et al. (2010) and Mirza et al. (2016). Subcaudal counts reported here do not include the terminal scale. The style of description follows Mirza et al. (2016) with some modifications. Abbreviations used to describe scalation and other comparable characters are: V, ventrals; PrV, preventrals; SC, subcaudals; DSR, dorsal scale rows; SVL, snout-vent length; TaL, tail length; TL, total length. Images were taken with the help of a Canon 700D camera using a Canon 100-mm macro lens and illumination using two Canon 430exII Speedlite flashes.

Lycodon deccanensis is primarily compared to the *Lycodon* species occurring in India and especially with members of the clade that *Lycodon deccanensis* belongs to, based on the molecular data. Abbreviations used in the manuscript: Bombay Natural History Society, Mumbai (BNHS); Muséum national d'Histoire naturelle, Paris (MNHN); National Centre for Biological Sciences, Bangalore (NCBS); Natural History Museum, London (NHM).

Molecular analysis

Genomic DNA was isolated from the preserved tissues of *Lycodon* spp. using Qiagen DNAeasy kits following protocols provided by the manufacturer. Sequences were generated for the two specimens of the *Lycodon deccanensis*, *L. striatus* from Savandurga, Karnataka and *L. flavicollis* from Devarayanadurga, Karnataka. A fragment of the mitochondrial cytochrome b (*cyt b*) gene was amplified. Published primers L14919 & H16064 (Burbrink et al. 2000) were used. A 22-µl reaction was set containing 10 µl of Thermo Scientific Dream Taq PCR Master Mix, 9 µl water, 0.5 µl of each primer, and 2 µl template DNA, carried out with an Eppendorf Mastercycler Nexus GSX1. Thermo-cycle s used for amplification were as follows: 94 °C for 5 min (denaturation temperature 94 °C for 30 s, annealing temperature 48 °C for 50 s, elongation temperature 72 °C for 1 min) × 30 cycles, 72 °C for 10 min, hold at 4 °C. PCR product was cleaned using a QIAquick PCR Purification Kit and sequenced with an AB 3730 DNA Analyzer. Taxa selected for the molecular phylogenetic analysis followed Zaher et al. (2019). Downloaded sequences were aligned in MegaX (Kumar et al. 2018) using ClustalW (Thompson et al. 1994) with default settings. For optimal partitioning strategy and evolutionary substitution model, aligned data was analyzed using PartitionFinder v. 1.1.1. (Lanfear et al. 2012). We conducted a Maximum Likelihood (ML) analysis to assess phylogenetic relationship with RAXML v. 1.5b1 (Silvestro and Michalak 2012). Data were subjected to phylogenetic reconstruction with the GTR+I+G model as the sequence substitution model, based on the optimal partitioning scheme suggested by PartitionFinder for both ML and Bayesian Inference (BI). ML was run for 1000 non-parametric bootstrap replicates with rapid ML search option. Bayesian Inference (BI) was implemented in MrBayes 3.2.2 (Ronquist and Huelsenbeck 2003) and was run for 10 million generations and sampled every 1000 generations. A BI run included five parallel chains, three

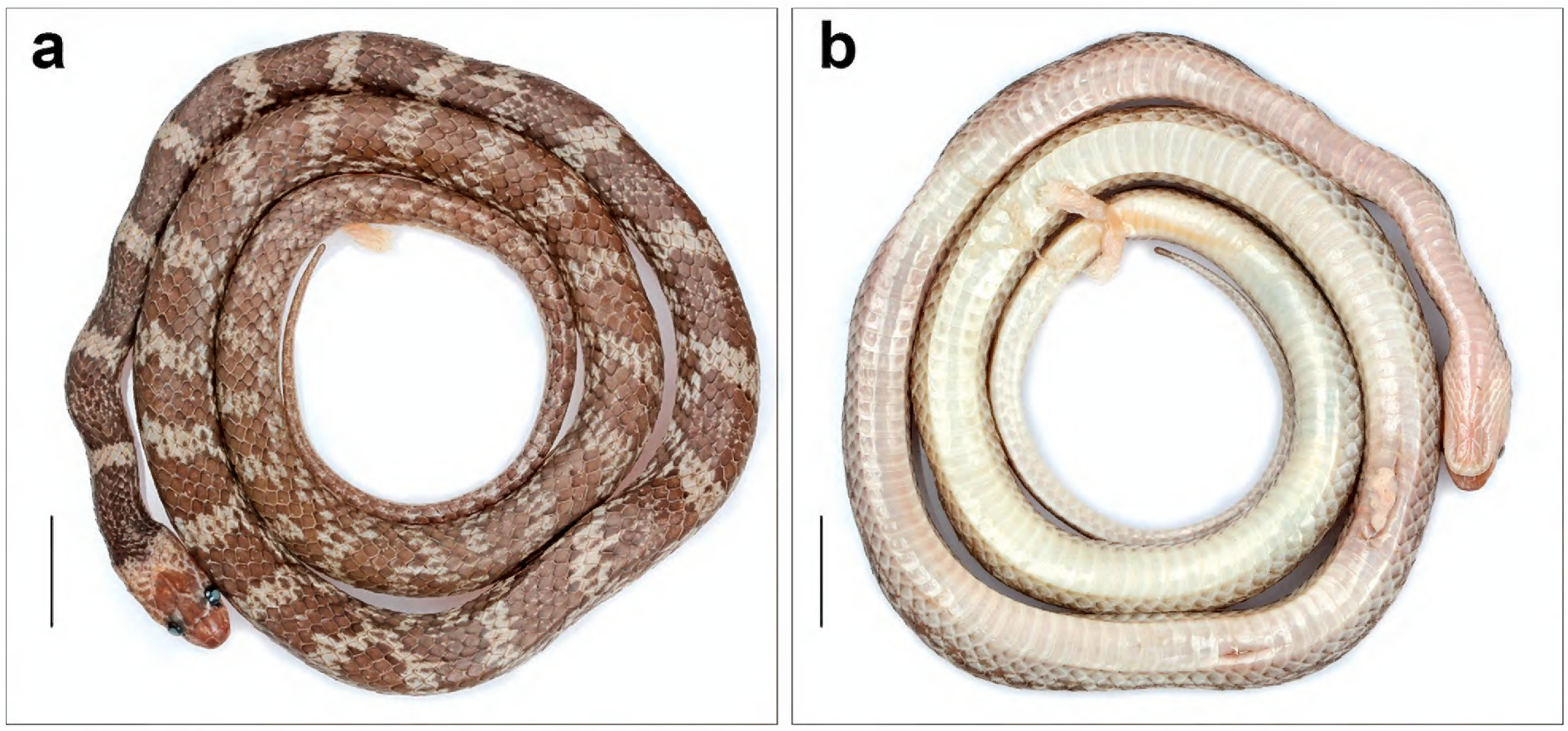

Figure 1. *Lycodon deccanensis* male NCBS NRC-AA-0010, (**a**) dorsal aspect, (**b**) ventral aspect. Scale bars: 10 mm.

hot and two cold chains. The run was terminated after the standard deviation of split frequencies of the analysis reached were < 0.05. Twenty-five percent of trees generated were discarded as burn-in. The tree was visualized and edited in FigTree (Rambaut 2012). The same dataset was subjected to phylogenetic analysis on the IQ-TREE (http://iqtree.cibiv.univie.ac.at) online portal (Minh et al. 2020) as it allows incorporation of several models not available in RAXML. Results from the IQ-TREE run are presented in the paper as the support values for the clades are higher than those form RAXML. Sequence accession numbers for sequences used in the phylogenetic analysis are listed in Suppl. material 1. A summary of the sequence substitution model used for different approaches for phylogenetics in presented in Suppl. material 5.

Results

Molecular phylogenetics based on 1111bp of the mitochondrial cytochrome b gene, *Lycodon deccanensis* was found to be a member of the genus *Lycodon* and was embedded within the *L. aulicus* clade. Morphological characters that include 17 DSR, laterally angulate ventral scales, loreal touching internasal and the arched maxilla (Smith 1943, Guo et al. 2013) further attest the relationship recovered based on molecular data. There is no intraspecific divergence observed for *cyt b* gene between the two specimens whereas interspecific divergence with its congeners is 14–17% (Table 1).

Examination of the images of the holotype BNHS 3596 shared by the Bombay Natural History Society confirms that the specimens collected by us are conspecific with *Lycodon deccanensis* in bearing an undivided anal shield, loreal in contact with internasal, preocular not in contact with frontal and the dorsal banding pattern. As per the description the holotype was preserved for eight years and has lost its dark colouration and has faded to light creamy brown and the bands are not as distinct (Ganesh et al. 2020a). However, the image of the holotype shared by the Bombay Natural History Society shows a specimen which clearly does not look old nor has the dark colouration faded (Suppl. material 6). It is unclear if the specimen whose images were sent to us is really the holotype as the holotype was not depicted in the paper. The paratype (ZSI 13271) of *Lycodon deccanensis* from South Arcot district, Tamil Nadu depicted in fig. 2b of Ganesh et al. (2020a) shows that the loreal shield is not in contact with the internasal and the preocular separates the supraocular and prefrontals a set of character states seen in *L. travancoricus* (Ganesh et al. 2020b, Smith 1943) and we here consider this specimen conspecific with *L. travancoricus*. In the variation section, Ganesh et al. (2020a) stated that the paratype agrees with the holotype, but as discussed earlier, it clearly does not. The authors provided a range of ventral and caudal scale counts but did not provide details for each individual. Given that the scale number ranges also included the range of *L. travancoricus*, these ranges cannot be relied upon and hence we here provide details of the freshly procured specimens.

Systematics

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Figs 1–4, Table 1

Material examined. adult male, NCBS NRC-AA-0010 collected from Devarayanadurga, Tumkur District, Karnataka, India (13.375778°N, 77.210972°E, elevation 1093 m, datum WGS84) by Yatin Kalki, Sachin Gowda, Manu Agnivamshi, Karthik Singh and Zeeshan A. Mirza on 17 June 2020. Adult female, BNHS 3601, collected from the same locality by Manu Agnivamshi, Sachin Gowda, Yatin Kalki and Zeeshan A. Mirza on 19 June 2020.

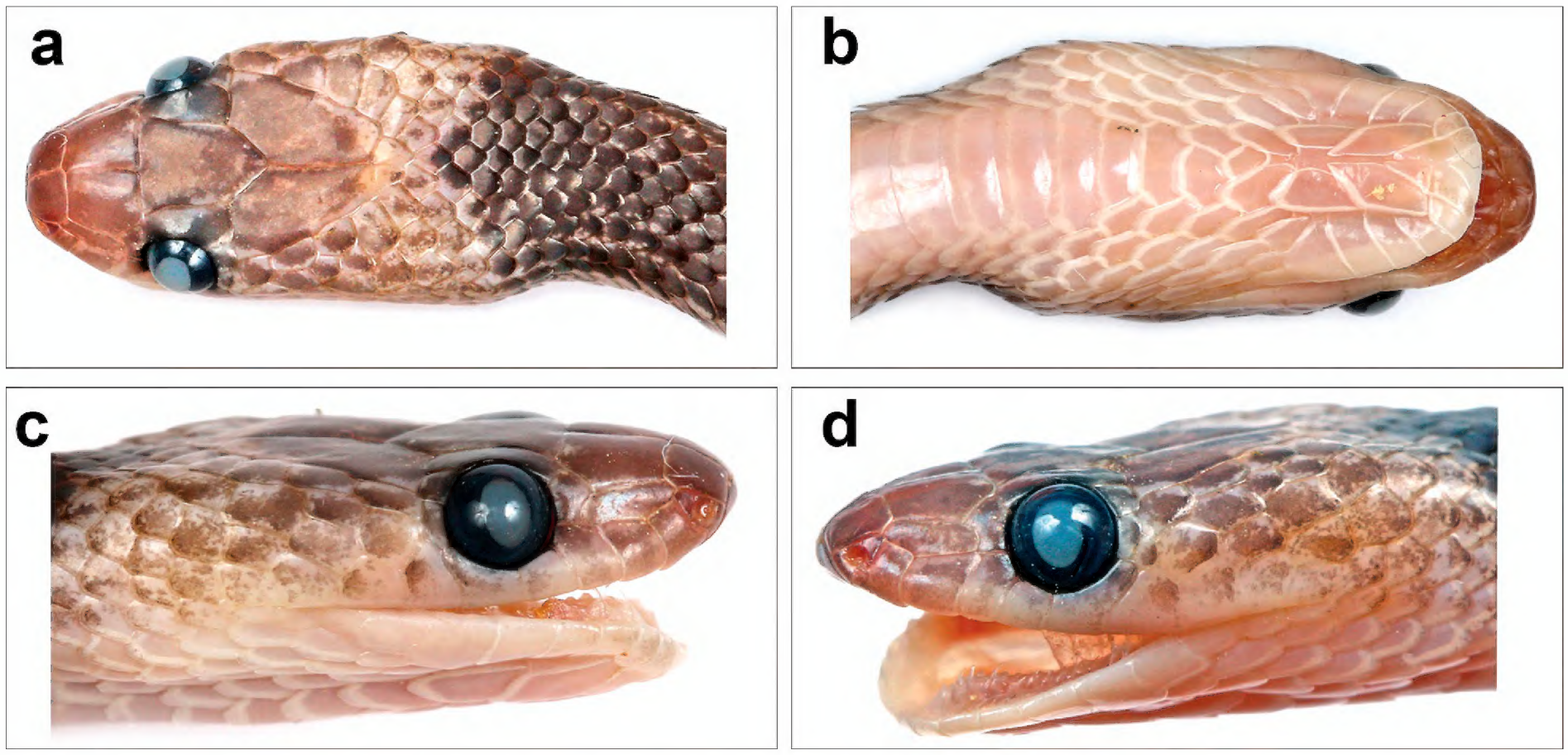

Figure 2. *Lycodon deccanensis* male NCBS NRC-AA-0010 showing head, (**a**) dorsal aspect, (**b**) ventral aspect, (**c**) right lateral aspect, (**d**) left lateral aspect.

Table 1. Uncorrected p-distance (sequence divergence) for members of the *Lycodon aulicus* clade.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	KC010346 *Lycodon aulicus*																		
2	KC010348 *Lycodon aulicus*	0.03																	
3	KC010350 *Lycodon aulicus*	0.05	0.05																
4	KC010355 *Lycodon capucinus*	0.05	0.05	0.03															
5	KC010356 *Lycodon capucinus*	0.05	0.05	0.02	0.04														
6	KC010359 *Lycodon capucinus*	0.03	0.00	0.05	0.05	0.05													
7	KC010376 *Lycodon effraenis*	0.18	0.19	0.19	0.19	0.18	0.19												
8	KC010364 *Lycodon effraenis*	0.20	0.20	0.20	0.20	0.20	0.20	0.14											
9	KC010367 *Lycodon jara*	0.17	0.15	0.16	0.17	0.16	0.15	0.21	0.19										
10	KC010368 *Lycodon laoensis*	0.18	0.17	0.17	0.17	0.17	0.17	0.16	0.15	0.18									
11	KC010370 *Lycodon laoensis*	0.18	0.17	0.17	0.17	0.17	0.17	0.16	0.15	0.18	0.02								
12	AF471040 *Lycodon zawi*	0.15	0.14	0.14	0.14	0.14	0.14	0.18	0.19	0.17	0.17	0.17							
13	KC010386 *Lycodon zawi*	0.13	0.12	0.14	0.13	0.13	0.12	0.17	0.18	0.15	0.16	0.16	0.02						
14	HQ735416 *Lycodon aulicus*	0.14	0.13	0.15	0.15	0.15	0.13	0.20	0.20	0.17	0.18	0.18	0.09	0.09					
15	MW006489 *Lycodon striatus*	0.17	0.17	0.17	0.17	0.17	0.17	0.17	0.16	0.16	0.13	0.13	0.16	0.15	0.17				
16	MW006488 *Lycodon flavicollis*	0.12	0.11	0.11	0.12	0.11	0.11	0.19	0.19	0.17	0.17	0.16	0.12	0.11	0.08	0.15			
17	MW006486 *Lycodon deccanensis*	0.16	0.16	0.17	0.17	0.17	0.16	0.18	0.19	0.16	0.17	0.17	0.16	0.15	0.17	0.14	0.16		
18	MW006487 *Lycodon deccanensis*	0.16	0.16	0.16	0.16	0.16	0.16	0.18	0.18	0.16	0.17	0.16	0.16	0.15	0.17	0.14	0.15	0.00	

Diagnosis (based on recently collected material). A small sized species of the genus *Lycodon* measuring SVL 300–350 mm, bearing 17 smooth DSR at midbody. Loreal in contact with internasal and preocular not in contact with frontal. Nine supralabials of which 3rd to 5th touch eye. Anal shield undivided. Ventrals 204–214 and subcaudals 66–69. Hemipenis cylindrical, not forked, with long spikes in distal half.

Comparison. *Lycodon deccanensis* differs from congeners recorded from India and those bearing 17 DSR from south Asia, in bearing the following different or non-overlapping characters: 17 smooth DSR at midbody (vs. 13 and 15 DSR in *L. nympha* and *L. gracilis* respectively, DSR keeled in *L. fasciatus* (Anderson, 1879), *L. gammiei* (Blanford, 1878) and *L. septentrionalis* (Gunther, 1875)), nine supralabials (vs. eight in *L. striatus*, *L. mackinnoni* Wall, 1906 and *L. fasciatus*, 6 or 7 in *L. nympha* and *L. gracilis*) ventrals 204–214 (vs. 174–186 in *L. anamallensis*, 165–183 in *L. flavomaculatus*, 167–188 in *L. jara* (Shaw, 1802), 218–237 in *L. tiwarii* Biswas & Sanyal, 1965, 176–206 in *L. travancoricus*, 154–195 in *L. striatus*, 163–187 in *L. laoensis* Gunther, 1864), anal plate undivided (divided in *L. aulicus*, *L. flavicollis*, *L. nympha*, *L. gracilis*, *L. striatus*, *L. anamallensis*, *L. flavomaculatus*, *L. hypsirhinoides* (Theobald, 1868)), a single preocular present (vs. preocular absent in *L. subcinctus* Boie, 1827), loreal in contact with internasal (vs. not in contact in *L. travancoricus* and *L. zawi* Slowinski, Pawar, Win, Thin, Gyi, Oo & Tun, 2001).

Description of male NCBS NRC-AA-0010 (Fig. 1). The specimen is in good condition preserved in a coil with its head resting outside the coil. The specimen bears two longitudinal incisions and hemipenes are partially everted (Fig. 1a, b).

Head short, measuring 12.3 mm from snout tip to the constriction at neck, comprising 3.39% of total length; high, 3.5 mm, with steeply domed snout in lateral view; upper jaw visible from ventral side. Head distinctly broad-

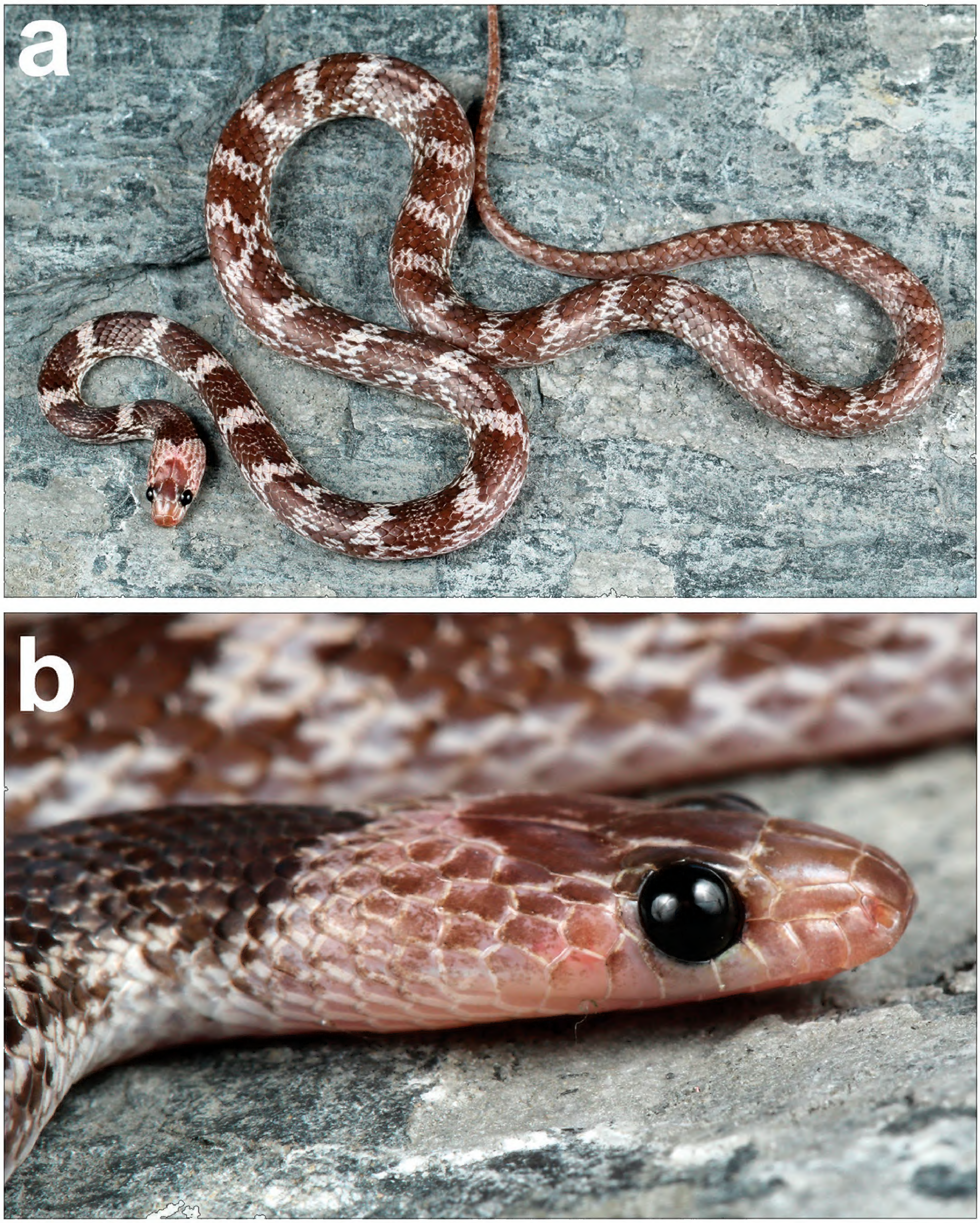

Figure 3. *Lycodon deccanensis* male NCBS NRC-AA-0010 in life showing dorsal patterning and colouration (**a**), close-up of the head (**b**). Photo by Zeeshan A. Mirza.

er (5.9 mm) than neck (3.7 mm). Snout gradually tapering to blunt, rounded tip in dorsal view (Fig. 2a). Rostral subtriangular, slightly visible when viewed from top; wider (1.3 mm) than deep (0.6 mm). Nostrils small, elliptical shaped, present in the basal region of the subtriangular nasal. Paired internasals, slightly wider (1.5 mm) than long (1.1 mm); smaller than prefrontals. Prefrontals, almost as long (1.8 mm) as wide (1.8 mm). Frontal bell shaped, 2.1 mm at the widest anterior border, median length 3.2 mm. Parietals 3.7 mm long, 2.6 mm at its widest anterior, 1.0 mm at its posterior border. Temporals 2+3+3 on right side and 2+3+4 on left side, subequal in size, poste-

Figure 4. *Lycodon deccanensis* female BNHS 3610 in life showing dorsal patterning and colouration. Photo by Zeeshan A. Mirza.

rior one inserts deeply between supralabial sixth, seventh and eighth. Six nuchal scales, slightly larger than adjacent dorsal scales, bordering parietals. Supraocular larger than preocular; preocular large, deeper (2.2 mm) than wide (1 mm). Loreal longer (1.4 mm) than high (0.7 mm). Two postoculars, upper one larger. Eye circular, 2.1 mm diameter with an elliptic pupil. Nine supralabials, third, fourth and fifth in contact with orbit (Fig. 2c, d). Supralabial I–III subequal in height and, apart from second supralabial, contacts only rostral and nasal. Second supralabial in contact with nasal, loreal and first + third supralabials. Fourth and fifth supralabials wider than high. Third supralabial in contact with preocular, second and forth supralabials and loreal. Sixth supralabial as high as the third supralabial.

Mental short, triangular. Infralabials 10, first really long, II to VI infralabials short and thin, fifth onwards larger (Fig. 1b). Seventh infralabial broadest and ninth much longest. First seven infralabials in contact with the genials. Anterior genials almost twice as long (2.4 mm) as wide (1.1 mm); posterior genials 1.1 mm long and 1 mm wide and in contact (Fig. 2b).

Body laterally compressed, ventral surface distinctly flattened. Dorsal scales in 17-17-15 rows. First lateral reduction observed after the 10th ventral is at 70% of the ventrals where third and fourth DSR are involved in reduction from 17 DSR to 15 at ventral 143. Dorsal scales imbricate, regularly arranged, vertebral scales not enlarged. All body scales smooth and glossy, with apical pit. Ventral scales 204 in number excluding three preventrals. Anal shield undivided, slightly larger than last ventral scale. Subcaudals paired, 68 in number. Tail terminates in a sharp, tapering apical spine. Total length 375 mm, tail length 75 mm, tail/total length ratio 0.2. Hemipenis cylindrical, not forked, with long spikes in distal half.

Colouration in preservative (Figs 1, 2). Background colour brown throughout, with more than 42 creamish white bands from the neck to the tail. The first band in at the neck forming a broad collar. Bands on the body about two dorsal scale width and the bands break-up towards the posterior part of the body to form reticulated pattern. Belly white lacking mottling or any marks. First two supralabials light brown with the rest predominantly white with a diffused brown patch in the center of each scale. Head shield darker than the labial scales. Three rows of scales bordering the pareital scales form the light collar band. Colouration in life more vivid and bright (Figs 3, 4). The dorsum is much darker and the dorsal bands are cream coloured. The colouration has faded after preservative.

Variation. The female BNHS 3610, agrees with the description of the male NCBS NRC-AA-0010 but differs in the attributes presented here: SVL 350 mm, TaL 78.5 mm, TL 428.5 mm, TaL/TL 0.18, V 214, Sc 66. Scale reduction from 17 DSR to 15 DSR observed at ventral 153 where scale rows 3 and 4 are involved.

Distribution. *Lycodon deccanensis* is currently recorded only from the type locality, Devarayanadurga, Karnataka, India, between elevations of 1000 meters and 1190 meters. Other locality records provided by Ganesh et al. (2020a) require verification based on voucher due to the misidentification of specimens as discussed above.

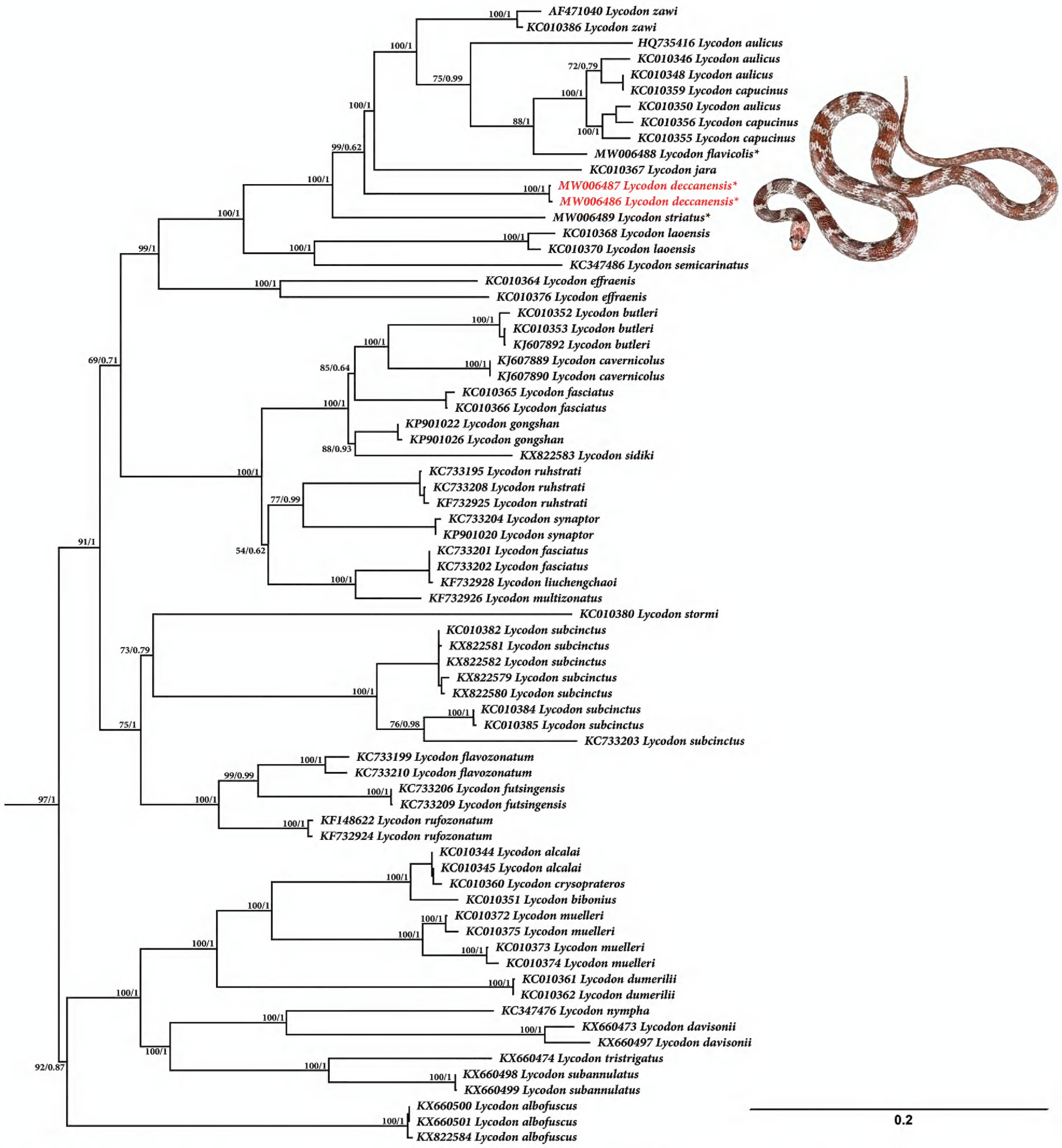

Figure 5. ML phylogeny of selected members of the genus *Lycodon* based on 1110 bp of mitochondrial cytochrome be gene reconstructed with IQ-TREE online portal. Numbers at nodes represent ML bootstrap support and BI posterior probability. For a complete tree, check supplementary material. Taxa marked with an '*' were generated in the present study.

Natural History. A total of six individuals have been found, one on 14 July 2019 and the remaining five between 10 June 2020 and 25 June 2020. All individuals were found between 2000 h and 0200 h, suggesting that the species is nocturnal like other *Lycodon* spp. Ventral scales with angulate lateral edges assist *L. deccanensis* in scaling the vertical surfaces of rocks, cliffs and walls. We observed one individual two meters high climbing on a relatively smooth wall and another individual 1.5 meters high that had taken refuge in a crevice in a stone pillar. One individual, which we kept in a container overnight, fed on a *Cnemaspis* cf. *mysoriensis* that it was offered. The following species have been observed in the same microhabitat sympatrically with *L. deccanensis*: *Cnemaspis* cf. *mysoriensis*, *Hemidactylus frenatus*, *H. parvimaculatus*, *H. whitakeri*, *Uperodon taprobanicus*, *U. variegatus*, *Boiga flaviviridis*, *Lycodon flavicollis*, and *L. gracilis*.

Discussion

Phylogenetic relationships recovered in the present study are congruent with that of Zaher et al. (2019) and Wostl et al. (2017) and *Lycodon deccanensis* is recovered as a member

of the *L. aulicus* group of Wostl et al. (2017) with high support for ML (bootstrap 99) with poor support in BI (posterior probability 0.62) (Fig. 5, Suppl. material 1–4). Due to lack of molecular data for most Indian representatives, relationships recovered in the present work may however change. Based on morphology, *Lycodon deccanensis* shows affinity to *Lycodon aulicus sensu lato* in bearing 17 DSR and the broad contact between the loreal and internasal shield. However, differs from all members of *Lycodon aulicus s. l.* in bearing an undivided anal shield a character state known only in *L. travancoricus* (Smith 1943, Ganesh and Vogel 2018, Patel et al. 2019). *Lycodon deccanensis* however, differs from all members of the *L. aulicus* clade in showing an un-corrected pairwise sequence divergence of 14–17% (Table 1).

The description of *Lycodon deccanensis* by Ganesh et al. (2020a) was a noteworthy attempt, however, the work presents erroneous voucher numbers, unsexed type specimens, multiple species in the type series, and a lack of molecular data.

Additionally, the recent revision of the *L. aulicus* group contingent on morphology alone by Ganesh and Vogel (2018) lacks molecular support to the taxonomic amendments and hence in our opinion cannot be relied upon largely because the group is morphologically cryptic and the study further lacks details of skull and dentition. Results based on molecular data are at odds with the current taxonomy and a detailed revision of the Indian members of the genus is needed.

Description of a distinct *Lycodon deccanensis* by Ganesh et al. (2020a) merely highlights the poor nature of documentation of snakes in a country as the whole, as several new species have been described in the last five years (Mirza et al. 2016, 2020, Giri et al. 2017, 2019, Bhosale et al. 2019, Deepak et al. 2020). Most of these descriptions were from biodiversity hotspots like the Western Ghats and the Himalayas whereas areas that lie outside biodiversity hotspots receive little attention. It is hoped that attempts are made to document the diversity of snakes across the country, especially in areas that are situated in unprotected dry lands or outside biodiversity hotspots. Recent herpetofaunal explorations of the Mysore plateau have demonstrated distinct and unique biota (Agarwal 2016, Mirza et al. 2018, Agarwal et al. 2020) and we advocate dedicated efforts to study the biodiversity of this region.

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References

Agarwal I (2016) Two new species of ground-dwelling *Cyrtodactylus* (*Geckoella*) from the Mysore Plateau, south India. Zootaxa 4193: 228–244. https://doi.org/10.11646/zootaxa.4193.2.2

Agarwal I, Thackeray T, Pal S, Khandekar A (2020) Granite boulders act as deep-time climate refugia: A Miocene divergent clade of rupicolous *Cnemaspis* Strauch, 1887 (Squamata: Gekkonidae) from the Mysore Plateau, India, with descriptions of three new species. Journal of Zoological Systematics and Evolutionary Research 58(4): 1234–1261. https://doi.org/10.1111/jzs.12391

Bhosale HS, Gowande G, Mirza ZA (2019) new species of fossorial natricid snakes of the genus *Trachischium* Günther, 1858 (Serpentes: Natricidae) from the Himalayas of northeast India. Comptes Rendus – Biologies 342: 323–329. https://doi.org/10.1016/j.crvi.2019.10.003

Burbrink FT, Lawson R, Slowinski JB (2000) Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): A critique of the subspecies concept. Evolution 54: 2107–2118. https://doi.org/10.1111/j.0014-3820.2000.tb01253.x

Das A, Mohapatra PP, Purkayastha J, Sengupta S, Dutta SK, Ahmed MF, Tillack F, Duméril B (2010) A contribution to *Boiga gokool* (Gray, 1835) (Reptilia: Squamata: Colubridae). Russian Journal of Herpetology 17: 161–178.

Deepak V, Narayanan S, Das S, Rajkumar KP, Easa PS, Sreejith KA, Gower DJ (2020) Description of a new species of *Xylophis* Beddome, 1878 (Serpentes: Pareidae: Xylophiinae) from the Western Ghats, India. Zootaxa 4755: 231–250. https://doi.org/10.11646/zootaxa.4755.2.2

Dowling H (1951a) A proposed method of expressing scale reductions in snakes. Copeia 2: 131–134. https://doi.org/10.2307/1437542

Dowling H (1951b) A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 11: 97–99.

Figueroa A, Mckelvy AD, Grismer LL, Bell CD (2016) A Species-Level Phylogeny of Extant Snakes with Description of a New Colubrid Subfamily and Genus. PLoS ONE 11: e0161070. https://doi.org/10.1371/journal.pone.0161070

Ganesh SR, Deuti K, Punith KG, Achyuthan NS, Mallik AK, Vogel G (2020a) A new species of *Lycodon* (Serpentes: Colubridae) from the Deccan Plateau of India, with notes on the range of *Lycodon travancoricus* (Beddome, 1870) and a revised key to peninsular Indian forms. Amphibian & Reptile Conservation 17(3): 74–84.

Ganesh SR, Amarasinghe AAT, Vogel G (2020b) Redescription of *Lycodon travancoricus* (Beddome, 1870) (Reptilia: Colubridae), an Indian endemic snake, with a review of its geographic range.

TAPROBANICA – The Journal of Asian Biodiversity 9: 50–58. https://doi.org/10.47605/tapro.v9i1.221

Ganesh SR, Vogel G (2018) Taxonomic reassessment of the Common Indian Wolf Snakes *Lycodon aulicus* (Linnaeus, 1758) complex (Squamata: Serpentes: Colubridae). Bonn Zoological Bulletin 67: 25–36.

Giri VB, Deepak V, Captain A, Das A, Das S, Rajkumar KP, Rathish RL, Gower DJ (2017) A new species of *Rhabdops* Boulenger, 1893 (Serpentes: Natricinae) from the northern Western Ghats region of India. Zootaxa 4319: 27–52. https://doi.org/10.11646/zootaxa.4319.1.2

Giri VB, Gower DJ, Das A, Lalremsanga HT, Lalronunga S, Captain A, Deepak V (2019) A new genus and species of natricine snake from northeast India. Zootaxa 4603: 241–264. https://doi.org/10.11646/zootaxa.4603.2.2

Guo P, Zhang L, Liu Q, Li C, Alexander Pyron R, Jiang K, Burbrink FT (2013) *Lycodon* and *Dinodon*: One genus or two? Evidence from molecular phylogenetics and morphological comparisons. Molecular Phylogenetics and Evolution 68: 144–149. https://doi.org/10.1016/j.ympev.2013.03.008

Janssen HY, Pham CT, Ngo HT, Le MD, Nguyen TQ, Ziegler T (2019) A new species of *Lycodon* Boie, 1826 (Serpentes, Colubridae) from northern Vietnam. ZooKeys 875: 1–29. https://doi.org/10.3897/zookeys.875.35933

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. Molecular Biology and Evolution 35: 1547–1549. https://doi.org/10.1093/molbev/msy096

Lanfear R, Calcott B, Ho S, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. Molecular Biology and Evolution 29: 1695–1701. https://doi.org/10.1093/molbev/mss020

Leary S, Underwood W, Anthony R, Cartner S (2013) AVMA guidelines for the euthanasia of animals. 2013 edn., 98 pp.

Luu VQ, Bonkowski M, Nguyen TQ, Le MD, Caíame T, Ziegler T (2020) A new species of *Lycodon* Boie, 1826 (Serpentes: Colubridae) from central Laos. Revue Suisse de Zoologie 125: 263–276. https://doi.org/10.11646/zootaxa.4586.2.3

Luu VQ, Ziegler T, Ha NV, Le MD, Hoang TT (2019) A new species of *Lycodon* Boie, 1826 (Serpentes: Colubridae) from Thanh Hoa Province, Vietnam. Zootaxa 4586: 261–277. https://doi.org/10.11646/zootaxa.4586.2.3

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, Haeseler A von, Lanfea R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Molecular Biology and Evolution 37: 1530–1534. https://doi.org/10.1093/molbev/msaa015

Mirza ZA, Bhosale HS, Phansalkar PU, Sawant M, Gowande GG, Patel H (2020) A new species of green pit vipers of the genus *Trimeresurus* Lacépède, 1804 (Reptilia: Serpentes: Viperidae) from western Arunachal Pradesh, India. Zoosystematics and Evolution 96: 123–138. https://doi.org/10.3897/zse.96.48431

Mirza ZA, Gowande G, Patil R, Ambekar M, Patel H (2018) First appearance deceives many: disentangling the *Hemidactylus triedrus* species complex using an integrated approach. PeerJ 6: e5341. https://doi.org/10.7717/peerj.5341

Mirza ZA, Vyas R, Patel H, Maheta J, Sanap RV (2016) A new Miocene-divergent lineage of Old World racer snake from India. PloS ONE 11(3): e0148380. https://doi.org/10.1371/journal.pone.0148380

Narayana BL, Sandeep M, Dogra S (2018) A new locality record for the Yellow-collared Wolfsnake, *Lycodon flavicollis* Mukherjee and Bhupathy 2007, from Hyderabad, Telangana, India. IRCF Reptiles and Amphibians Conservation and Natural History 25: 55–56.

Patel H, Vyas R, Pranav V (2019) On the distribution of *Ahaetulla laudankia* Deepak, Narayanan, Sarkar, Dutta & Mohapatra, 2019 and *Lycodon travancoricus* (Beddome, 1870) (Squamata, Colubridae) from Gujarat, India. Check List 15: 1045–1050. https://doi.org/10.15560/15.6.1045

Rambaut A (2012) FigTree v.1.4.3. http://tree.bio.ed.ac.uk/software/figtree/

Ronquist F, Huelsenbeck J (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Silvestro D, Michalak I (2012) raxmlGUI: a graphical front-end for RAxML. Organisms Diversity & Evolution 12: 335–337. https://doi.org/10.1007/s13127-011-0056-0

Smith MA (1943) Fauna of British India, Ceylon and Burma, including the whole of the Indo-Chinese Sub-region. Reptilia and Amphibia. Vol. 3. Serpentes. Taylor and Francis, London, 583 pp.

Thompson J, Higgins D, Gibson T (1994) ClustalW: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673–4680. https://doi.org/10.1093/nar/22.22.4673

Uetz P, Hošek J (2020) The Reptile Database. http://www.reptile-database.org [October-20-2020]

Vogel G, David P (2019) A new species of the *Lycodon fasciatus* complex from the Khorat Plateau, eastern Thailand (Reptiles, Squamata, Colubridae). Zootaxa 4577: 515–528. https://doi.org/10.11646/zootaxa.4577.3.6

Wallach V, Williams K, Boundy J (2014) Snakes of the World: A catalogue of living and extinct species. Taylor & Francis Group, London, 1257 pp. https://doi.org/10.1201/b16901

Whitaker R, Captain A (2004) Snakes of India. The field guide. Draco Books, Chennai, 481 pp.

Wickramasinghe LM, Vidanapathirana DR, Pushpamal V, Wickramasinghe N (2020) A new species of *Dryocalamus* (Serpentes: Colubridae) endemic to the rainforests of southwestern Sri Lanka. Zootaxa 4748: 248–260. https://doi.org/10.11646/zootaxa.4748.2.2

Wostl E, Hamidy A, Kurniawan NIA, Smith EN (2017) A new species of Wolf Snake of the genus *Lycodon* H. Boie in Fitzinger (Squamata: Colubridae) from the Aceh Province of northern Sumatra, Indonesia. Zootaxa 4276: 539–553. https://doi.org/10.11646/zootaxa.4276.4.6

Zaher H, Murphy RW, Arredondo JC, Graboski R, Machado-Filho PR, Mahlow K, Montingelli GG, Quadros AB, Orlov NL, Wilkinson M, Zhang YP, Grazziotin FG (2019) Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). PLoS ONE 14(5): e0216148. https://doi.org/10.1371/journal.pone.0216148

Supplementary material 1

List of species and their sequence accession numbers used in the study

Authors: Yatin Kalki, Sachin Gowda, Manu Agnivamshi, Karthik Singh, Harshil Patel, Zeeshan A. Mirza
Data type: molecular data
Explanation note: Accession numbers in bold belong to sequences generated in the present study.
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Link: https://doi.org/10.3897/evolsyst.4.60570.suppl1

Supplementary material 2

ML phylogeny of selected members of the family Colubriade based on 1110 bp of mitochondrial cytochrome be gene reconstructed with IQ-TREE online portal

Authors: Yatin Kalki, Sachin Gowda, Manu Agnivamshi, Karthik Singh, Harshil Patel, Zeeshan A. Mirza
Data type: Phylogeny
Explanation note: Numbers at nodes represent ML bootstrap support.
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Link: https://doi.org/10.3897/evolsyst.4.60570.suppl2

Supplementary material 3

ML phylogeny of selected members of the family Colubriade based on 1110 bp of mitochondrial cytochrome be gene reconstructed with RAXML

Authors: Yatin Kalki, Sachin Gowda, Manu Agnivamshi, Karthik Singh, Harshil Patel, Zeeshan A. Mirza
Data type: Phylogeny
Explanation note: Numbers at nodes represent ML bootstrap support.
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Supplementary material 4

BI phylogeny of selected members of the family Colubriade based on 1110 bp of mitochondrial cytochrome be gene reconstructed with MrBayes

Authors: Yatin Kalki, Sachin Gowda, Manu Agnivamshi, Karthik Singh, Harshil Patel, Zeeshan A. Mirza
Data type: Phylogeny
Explanation note: Numbers at nodes represent BI posterior probability.
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Link: https://doi.org/10.3897/evolsyst.4.60570.suppl4

Supplementary material 5

Sequence substitution model used in phylogenetic analysis for cyt b gene

Authors: Yatin Kalki, Sachin Gowda, Manu Agnivamshi, Karthik Singh, Harshil Patel, Zeeshan A. Mirza
Data type: Sequence substitution model
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Link: https://doi.org/10.3897/evolsyst.4.60570.suppl5

Supplementary material 6

Images of the holotype of *Lycodon deccanensis*. Courtesy Rahul Khot (BNHS)

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Data type: JPG Images
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